



Postnatal growth of forelimb musculo-tendinous systems in sigmodontine rats (Rodentia: Cricetidae)

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The musculo-tendinous system is responsible for generating and transmitting forces necessary to produce and control body movements. The focus of this study was to investigate ontogenetic patterns in the growth of forelimb muscles and tendons in 4 sigmodontine rodents (ambulatory *Akodon*, quadrupedal saltatorial *Eligmodontia*, scansorial *Oligoryzomys*, and semifossorial *Oxymycterus*) and to discover if these patterns differ with respect to species–locomotor mode. We examined forelimbs of 64 specimens including juveniles, young adults, and adults, and removed and measured 12 muscles and 7 tendons. The evolution of morphology is reflected in both static and ontogenetic allometric patterns. The general allometric pattern revealed by our data is one of decreased growth rate with larger size, because all morphological variables exhibit negative allometry. Patterns of allometry in the musculo-tendinous system may represent adaptations to specific habitat requirements. These patterns differed among species, and hence among locomotor types: 7 morphological variables showed subtle differences between species–locomotor types, while the trends within 3 species–locomotor types did not differ. The strongest patterns were associated to the muscles and tendons related to extension of the arm and flexion of the wrist.

El sistema músculo-tendinoso es el responsable de generar y transmitir la fuerza necesaria para producir y controlar los movimientos en los organismos. El objetivo principal de nuestro estudio fue investigar el crecimiento relativo de las estructuras músculo-tendinosas del miembro anterior a lo largo de la ontogenia en cuatro roedores sigmodontinos (*Akodon* ambulatorio, *Eligmodontia* cuadrúpedo saltatorial, *Oligoryzomys* escansorial y *Oxymycterus* excavador) y evaluar si los patrones de crecimiento correspondientes difieren en cuanto al tipo predominante de locomoción. Para ello, se examinaron miembros anteriores de 64 ejemplares pertenecientes a diferentes edades: juveniles, adultos jóvenes y adultos, y se extrajeron y midieron 12 músculos y 7 tendones. La evolución de la morfología se refleja en los patrones alométricos estáticos y ontogenéticos. Nuestros datos muestran un patrón general de crecimiento alométrico con una disminución en la tasa de crecimiento con relación al incremento del tamaño corporal, ya que todas las variables morfológicas exhiben alometría negativa. Los patrones de alometría en el sistema músculo-tendinoso pueden representar adaptaciones a los requerimientos específicos del hábitat que los organismos explotan. Estos patrones difieren entre las especies, y por lo tanto entre diferentes tipos locomotores: 7 variables morfológicas mostraron sutiles diferencias entre los tipos de locomoción, mientras que las tendencias dentro de 3 especies–tipos locomotores no difieren. Los patrones más fuertes se asociaron a los músculos y tendones relacionados con la extensión del brazo y la flexión de la muñeca.

Key words: locomotor modes, musculo-tendinous morphology, ontogeny, Sigmodontinae

Studies of mammalian ontogeny have focused on skulls (Leamy and Atchley 1984; Radinsky 1984; Gianinni et al. 2004, 2010; Flores et al. 2010, 2013; Verzi et al. 2010; Cassini et al. 2012, 2015; Segura 2013, 2015; Del Castillo et al. 2014; Vassallo et al. 2015; Moyano and Gianinni 2017), postcranial skeletons (Nesslinger 1956; Leamy and Bradley 1982; Shea 1992; Ruff et al. 1994; Eilam 1997; Maunz and German 1997; Lammers and German 2002; Prochel and Sanchez-Villagra 2003; Prochel 2006; Schilling and Petrovitch 2006; Young 2006; Kilbourne and Makovicky 2012; Echeverría et al. 2014; Fosse and Cregut-Bonnoure 2014), or the muscular system (Crawford 1954; Carrier 1983; Lodder et al. 1994; Tamaki and Uchiyama 1995; Atzeva et al. 2007; Barros et al. 2009; Diogo et al. 2014). Using comparative descriptions, geometric morphometrics, or allometric analyses, these works identified ontogenetic patterns related to behavior (e.g., change in diet), functional factors (e.g., locomotor specialization), and phylogenetic history. Understanding patterns of ontogenetic variation within the musculo-tendinous system is important because this system is responsible for generating and transmitting the forces necessary to produce and control body movements (Biewener 1998; Böl et al. 2017).

Haines (1932) identified “the laws of muscle and tendon growth” based mainly on observations of human development. He proposed that tendons increase in length through muscle metamorphosis, and showed that in late fetal stages musculature is very similar to that of the adult, but there is a relatively greater proportion of muscle compared to tendon. Similarly, other authors have shown that during growth the architecture and dimensions of muscles change with body weight or bone length. Comer (1956) analyzed ontogenetic changes in the gastrocnemius of laboratory rats (*Rattus norvegicus*) relative to lengths of the muscle belly, tendon, and tibia. He observed that in contrast to tendon length, muscle belly length depends on the range of motion and growth rate of the tibia. Alder et al. (1958) found that in rabbits (*Oryctolagus cuniculus*) the growth rate of the belly of the m. tibialis anterior is slightly higher than that of its tendon, because the tension that the muscle can exert in full dorsiflexion of the foot is relatively greater in adults than in young individuals. De Koning et al. (1987) studied growth of both the gastrocnemius and tibialis anterior muscles in rats and noted that muscle length, tendon length, and their relationships change considerably with age. Böl et al. (2017) postulated that the muscle, tendon, and geometry of the aponeurosis of the rabbit shank musculature follow an almost linear growth pattern. Most studies on ontogenetic patterns of muscles and tendons have focused on hindlimbs of wistar rats, an albino strain of laboratory rat (Woittiez et al. 1985, 1986; Alnaqeeb and Goldspink 1987; De Koning et al. 1987; Heslinga and Huijing 1990; Barros et al. 2009).

Within mammals, rodents are phylogenetically and morphologically diverse. In South America, the greatest diversity of rodents is found in the subfamily Sigmodontinae (Cricetidae), represented by about 86 genera and more than 400 living species (Patton et al. 2015), and constitutes a recent adaptive radiation that began in the middle Miocene (9–12 Mya—Parada

et al. 2015). They are diverse ecologically and in terms of locomotor mode, and thus are able to occupy varied habitats including wet tropical and temperate forests, wetlands, scrublands, savannas, steppes, high elevations, grasslands, deserts, and salt flats (Hershkovitz 1962; Voss 1988; Rivas and Linares 2006; Weksler 2006; Rivas et al. 2010). The species richness and ecomorphological diversity within the Sigmodontinae presents an ideal system in which to study ontogenetic patterns.

To date, studies of growth and development in the Sigmodontinae have focused on osteological architecture (Creighton and Strauss 1986; Voss and Marcus 1992; Eilam 1997; Hingst-Zaher et al. 2000; López-Fuster et al. 2001; Breno et al. 2011; Prado and Perciquillo 2011; Maestri et al. 2015; Hernandez et al. 2017). In this study, we analyzed post-natal ontogenetic variation of the musculo-tendinous system in sigmodontine species with different locomotor modes. In our data, species and locomotor mode are confounded. However, the possibility that species have diversified as a consequence of different locomotor challenges cannot be discounted. Taking this possibility into consideration our objectives were: 1) to identify the relative growth trajectories of muscular and tendinous structures of the forelimb, and 2) to analyze these patterns in the context of the locomotor modes exhibited by the selected species of sigmodontine rats.

MATERIALS AND METHODS

We analyzed 64 specimens preserved in alcohol belonging to 4 Sigmodontinae genera: *Akodon*, *Eligmodontia*, *Oligoryzomys*, and *Oxymycterus* (Fig. 1), each exhibiting different types of locomotion. We distinguished 3 age classes based on molar eruption sequence and extent of wear (Patterson 1992; Oliveira et al. 1998:23): juvenile (stage 2), young adult (stage 3), and adult (stage 4). Our sample included 23 juveniles (8 *Akodon*, 7 *Eligmodontia*, 2 *Oligoryzomys*, 6 *Oxymycterus*), 29 young adults (6 *Akodon*, 14 *Eligmodontia*, 3 *Oligoryzomys*, 6 *Oxymycterus*), and 12 adults (3 *Akodon*, 3 *Eligmodontia*, 3 *Oligoryzomys*, 3 *Oxymycterus*). Specimens examined were deposited in collections listed in Appendix I.

For each specimen the right forelimb was dissected and 12 muscles and 7 tendons (Table 1) were removed intact and measured (Fig. 2). Total muscle and tendon lengths (m, TL) were measured between the corresponding origin and insertion points; the maximum width of each tendon (TW) was also recorded at approximately the midpoint of the origin of the tendon. For muscles and tendons, the nomenclature of Rinker (1954) and Diogo et al. (2009) was followed. All measurements, including body length, were taken in mm using a digital caliper. The data are provided in Supplementary Data SD1.

To estimate ontogenetic scaling of muscles and tendons of the forelimb, we used 26 morphological variables representing muscle lengths and lengths and widths of tendons for extensors and flexors, as well as body length (Table 1; Supplementary Data SD1). Assumptions about normality and homoscedasticity of variance were checked graphically and using the Kolmogorov–Smirnov test. Data were log₁₀-transformed before

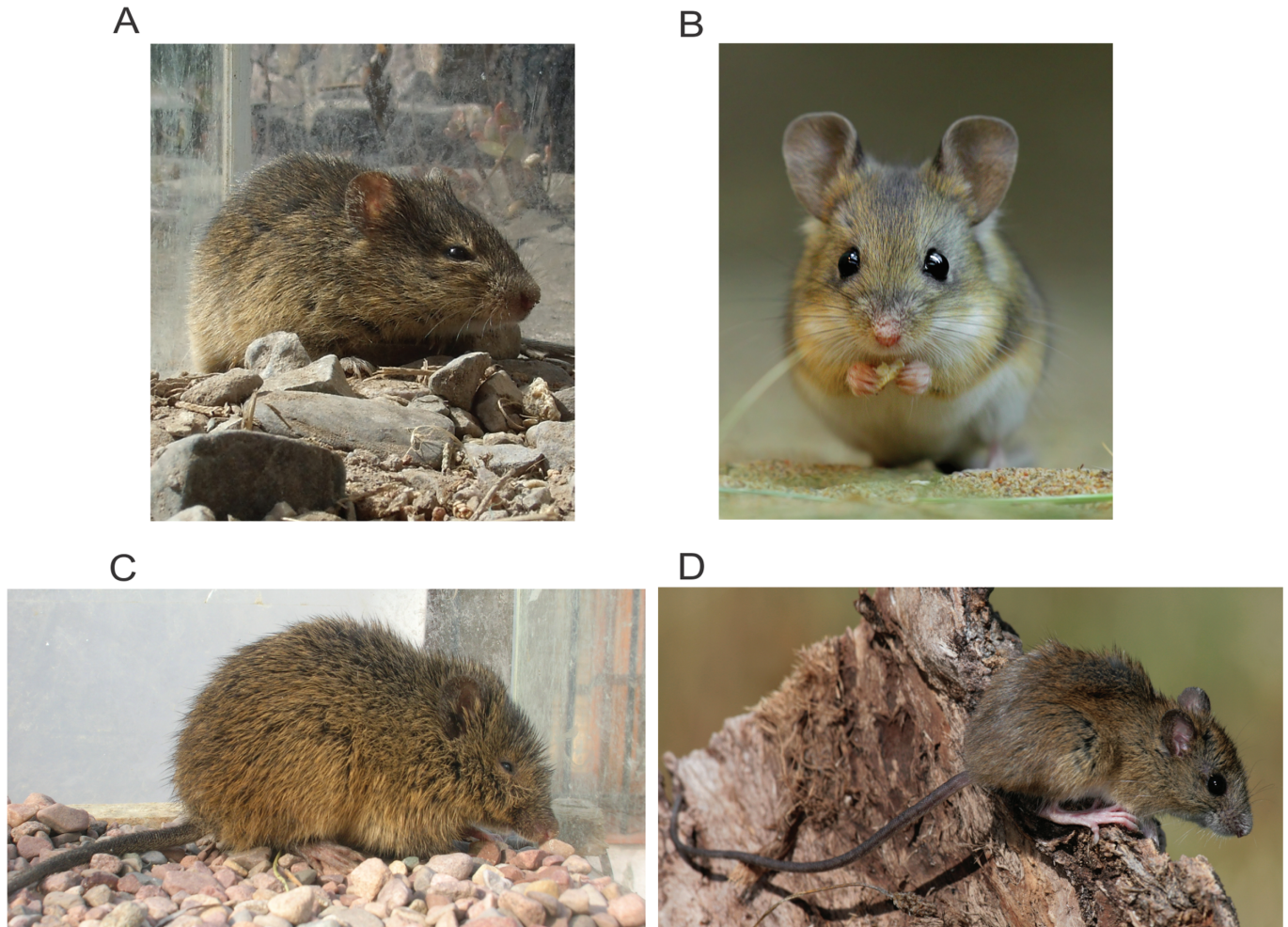


Fig. 1.—Sigmodontine species analyzed: A) *Akodon caenosus*, ambulatory form; B) *Eligmodontia typus*, quadrupedal saltatorial form; C) *Oxymycterus rufus*, semifossorial form; D) *Oligoryzomys longicaudatus*, scansorial form.

Table 1.—List of forelimb muscles and tendons for 4 species of sigmodontine rodents (*Akodon caenosus*, *Eligmodontia typus*, *Oligoryzomys longicaudatus*, and *Oxymycterus rufus*). TL: tendon length; TW: tendon width.

Muscles	Abbreviations	Tendon	Abbreviations	Group
Extensor				
Triceps brachii, caput longus	Tlon			Triceps
Triceps brachii, caput lateralis	Tlat			Triceps
Triceps brachii, caput medialis	Tmed			Triceps
Extensor carpi radialis	ECRad	x	TLECRad/TWECRad	Extensor of the forearm
Extensor carpi ulnaris	ECUln	x	TLECUln/TWECUln	Extensor of the forearm
Extensor digitorum communis	EDCom	x	TLEDCom/TWEDCom	Extensor of the forearm
Flexor				
Biceps brachii	BB			Flexor of the arm
Brachialis	B			Flexor of the arm
Flexor carpi radialis	FCRad	x	TLFCRad/TWFCRad	Flexor of the forearm
Flexor carpi ulnaris	FCUln	x	TLFCUln/TWFCUln	Flexor of the forearm
Flexor digitorum profundus	FDProf	x	TLFDProf/TWFDProf	Flexor of the forearm
Flexor digitorum sublimis	FDSubl	x	TLFDSubl/TWFDSubl	Flexor of the forearm

subsequent analyses. Principal component analysis (PCA) was used as an ordination tool. PC scores were used to assess and quantify overall differences in general body size and shape. From the PCA we obtained the first eigenvector that expresses the allometric relationships among all variables with latent size;

this eigenvector is extracted from a variance–covariance matrix of log-transformed variables and scaled to unity (Jolicoeur 1963). We repeated the regression with PC1 as a covariate to explore relationships among variables using comparable bivariate analyses. Next, we performed a series of bivariate analyses

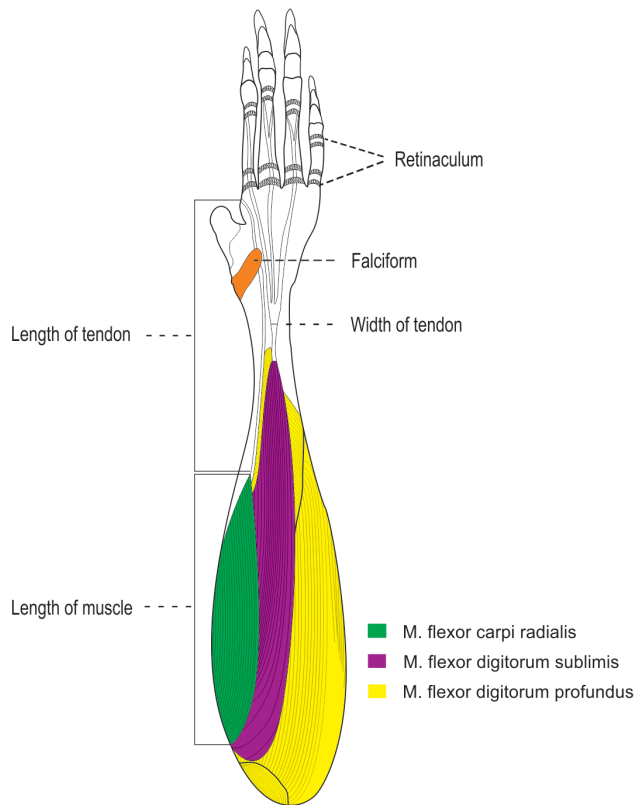


Fig. 2.—Ventral view of the left forelimb in the sigmodontine rodent *Akodon caenosus* showing measurements of the muscles and tendons used in this study.

to evaluate the growth trends of morphological variables in each species.

Multiple linear stepwise regression with a forward selection routine was used to assess growth patterns among morphological variables in each species against size (defined by PC1). Variable selection within the forward selection routine was based on Mallows's P (Mallows 1973; Gilmour 1996) and the coefficient of determination. To do this, we used the leaps package for R (R version 3.4.1—R Development Core Team 2013). The leaps () function searches for the best subset of predictors using Mallows's P statistic, an indicator of bias. The models with the lowest values of Mallows's P are similar to those with the highest values of adjusted R^2 . Ideally, the value of Mallows's P approaches the number of parameters in the model without being smaller than the number of parameters. The objective of this process is to build the most parsimonious model with the greatest explanatory power and minimal bias. We used the stepwise regression approach to select variables for an assessment of allometry using reduced major axis (RMA) regression.

To determine allometric relationships, a bivariate RMA (model II) regression analysis was performed with variables identified using the stepwise selection routine against PC1 as a proxy for body size. Confidence intervals (CIs) for regression slopes were generated using a bootstrapping routine (10,000 replicates). If the CI excluded a value of 1.0 (the slope expected for isometric growth for linear measurements versus PC1), then allometry (i.e., a departure from isometry) was considered

significant. Thus, negative allometry was indicated by slopes significantly < 1.0 , positive allometry by slopes significantly > 1.0 , and isometry by slopes not different from 1.0. We used an alpha level of 0.05 for all statistical tests. Statistical analyses were performed using PAST 3.14 (Hammer et al. 2001).

Although we are aware that sigmodontine rodents are capable of a wide range of locomotor modes, we assigned a specific locomotor mode to each of our species on the basis of their most frequent activity. This was determined based on habitat preferences, and was compiled from the literature and field observations (Myers and Carleton 1981; Hershkovitz 1994; Emmons and Feer 1999; Taraborelli et al. 2003). Classification of locomotor modes follows Carrizo et al. (2014); ambulatory species usually move on the ground and do not have specializations that facilitate or limit any particular activity (e.g., *Akodon caenosus*); in quadrupedal saltatorial species the forelimbs alternate with the hindlimbs in striking the ground simultaneously (e.g., *Eligmodontia typus*); scansorial species climb vertical surfaces by pulling their forefeet toward the substrate while the hind feet push on the substrate (e.g., *Oligoryzomys longicaudatus*); semifossorial species regularly dig to build simple burrows as shelters using mainly their forelimbs (e.g., *Oxymycterus rufus*).

We analyzed changes during postnatal ontogeny for 26 log-transformed morphological variables using a multivariate analysis of covariance (MANCOVA). Factors used in the MANCOVA were: age classes, species, and the age class by species interaction. Each morphological trait was used as a dependent variable and PC1 score was used as a covariate reflecting latent size (Giannini et al. 2004, 2010; Segura and Prevosti 2012; Jayat et al. 2017). Statistical analyses were performed using PAST 3.14 (Hammer et al. 2001). We estimated the false discovery rate (FDR) to determine which means were significantly different from one another (García 2003; Moran 2003; Nakagawa 2004). This approach is less conservative than the Bonferroni adjustment and tends to decrease the type I error rate (Weller et al. 1998; Benjamini and Yekutieli 2001; Waite and Campbell 2006). FDR tests were computed using R (R version 3.4.1—R Development Core Team 2013).

RESULTS

Musculo-tendinous allometry.—*Akodon caenosus*: The multiple regression for *A. caenosus* produced an R^2 value of 0.29. The overall regression was significant ($F_{1,15} = 1.468$; $P < 0.04$). Six variables recovered by the model (Mallows's $P = 13.60$) were related to muscle length: m. triceps longus (Tlon), m. triceps lateralis (Tlat), m. brachialis (B), m. extensor carpi radialis (ECRad), m. flexor digitorum profundus (FDProf), m. flexor carpi radialis (FCRad); and 8 were related to tendon length and width: m. extensor digitorum communis tendon width (TWEDCom), m. extensor carpi ulnaris tendon length and width (TLECUln and TWECUln), m. flexor carpi ulnaris tendon length and width (TLFCUln and TWFCUln), m. extensor carpi radialis tendon length (TLECRad), m. flexor digitorum profundus tendon width (TWFDProf), m. flexor carpi radialis tendon width (TWFCRad). A bivariate RMA regression

showed that only 4 of the analyzed morphological variables deviated significantly from isometry; all showing negative allometry (Table 2).

Eligmodontia typus: The coefficient of determination for the multiple regression was large ($R^2 = 0.971$) and the regression was significant ($F_{1,22} = 751.4$; $P < 0.001$). Nine variables recovered by the model (Mallows's $P = 21.62$) were related

to muscle length: Tlon, Tlat, m. triceps medialis (Tmed), m. biceps brachii (BB), B, ECRad, m. flexor carpi ulnaris (FCUln), m. flexor digitorum sublimis (FDSubl), m. extensor carpi ulnaris (ECUln); and 12 were related to tendon length and width: m. extensor digitorum communis tendon length and width (TLEDCom and TWEDCom), TLECUln and TWECUln, m. extensor carpi radialis tendon length and width (TLECRad

Table 2.—Results of the reduced major axis (RMA) regression describing ontogenetic growth of morphological variables (muscles and tendons) in each species. (–) denotes negative allometry. Significant P -values (< 0.05) are indicated with bold font. Correlation coefficient is shown with r . $CI = 95\%$ confidence interval. Acronyms are defined in Table 1.

Species	Morphological variables	Slope	Intercept	Slope CI limits	r	P
<i>Akodon caenosus</i>	Tlon	0.280	0.916	–0.097 to 1.195	0.299	0.255
	Tlat	0.257	0.901	–0.988 to 0.201	–0.134	0.607
	B	–0.234 (–)	0.821	–0.893 to –0.109	–0.520	0.032
	TWEC	0.428 (–)	–0.595	–0.103 to 1.365	0.509	0.036
	TLECUln	–0.149	0.866	–0.594 to 0.048	–0.422	0.084
	TWECUln	–0.633 (–)	–0.812	–0.915 to 0.160	–0.548	0.020
	ECRad	–0.252	0.790	–1.021 to 0.023	–0.422	0.091
	TLECRad	–0.196	0.850	–0.545 to 0.044	–0.354	0.165
	FDProf	0.209	0.771	0.110 to 0.965	0.064	0.826
	TWFDProf	0.182	–0.212	–0.825 to 0.014	–0.256	0.321
	TFCUln	–0.201	0.836	–0.881 to 0.069	–0.240	0.367
	TWFCUln	–0.550 (–)	–0.805	–0.731 to 0.227	–0.578	0.011
	FCRad	–0.340	0.716	–1.117 to 0.241	–0.040	0.875
	TWFCRad	–0.385	–0.922	–1.309 to 0.272	–0.039	0.880
<i>Eligmodontia typus</i>	Tlon	0.195 (–)	0.896	0.128 to 0.237	0.841	0.0001
	Tlat	0.178 (–)	0.867	0.121 to 0.223	0.831	0.0001
	Tmed	0.235 (–)	0.851	0.164 to 0.289	0.839	0.0002
	BB	0.378 (–)	0.660	0.272 to 0.454	0.862	0.0001
	B	0.431 (–)	–0.632	0.337 to 0.533	0.867	0.0001
	TLECom	0.210 (–)	0.870	0.133 to 0.257	0.818	0.0001
	TWECCom	0.180 (–)	0.817	0.121 to 0.223	0.663	0.0008
	ECUln	0.178 (–)	0.868	0.102 to 0.228	0.578	0.002
	TLECUln	0.370 (–)	–0.621	0.297 to 0.438	0.844	0.0001
	TWECUln	0.154 (–)	0.797	0.108 to 0.193	0.595	0.002
	ECRad	0.118 (–)	0.833	0.083 to 0.152	0.713	0.0001
	TLECRad	0.352 (–)	–0.741	0.264 to 0.426	0.796	0.0001
	TWECRad	0.157 (–)	0.766	0.100 to 0.203	0.654	0.0008
	TLFDProf	0.179 (–)	0.789	0.121 to 0.218	0.759	0.0001
	TWFDProf	0.119 (–)	0.869	0.074 to 0.147	0.765	0.0001
	FCUln	0.651 (–)	–0.543	0.270 to 1.042	0.650	0.0007
	TLFCUln	0.161 (–)	0.849	0.094 to 0.218	0.583	0.003
	TWFCUln	0.369 (–)	–0.769	0.261 to 0.455	0.566	0.004
	TLFCRad	0.195 (–)	0.878	0.128 to 0.244	0.570	0.004
TWFCRad	0.350	–0.763	0.126 to 1.142	0.221	0.298	
FDSubl	0.223 (–)	0.807	0.149 to 0.278	0.851	0.0001	
<i>Oligoryzomys longicaudatus</i>	Tlon	0.199	0.989	–0.060 to 0.298	0.606	0.109
	ECRad	0.192 (–)	0.826	0.078 to 0.284	0.824	0.016
	FDProf	0.210 (–)	0.908	0.104 to 0.311	0.773	0.019
	TWFCRad	0.485 (–)	–0.797	0.256 to 0.805	0.836	0.018
	TLFDSubl	0.235 (–)	0.910	0.088 to 0.295	0.869	0.0009
	TLFCUln	0.22	0.856	0.069 to 0.729	0.374	0.361
<i>Oxymycterus rufus</i>	Tlon	0.181 (–)	1.164	0.063 to 0.229	0.804	0.0007
	ECRad	0.172 (–)	1.068	0.082 to 0.218	0.684	0.006
	FDProf	0.137	1.107	0.044 to 0.195	0.476	0.088
	TLFCUln	0.171 (–)	0.912	0.065 to 0.229	0.762	0.001
	TWFCRad	0.378 (–)	–0.430	0.152 to 0.522	0.657	0.011
	TLFDSubl	–0.730	0.898	–1.822 to –0.473	–0.555	0.069

and TWECRad), TLFCUln and TWFCUln, m. flexor carpi radialis tendon length (TLFCRad), m. flexor digitorum sublimis tendon width (TWFDSubl), m. flexor digitorum profundus tendon length and width (TLFDProf and TWFDProf). The RMA regression showed that 20 of the analyzed morphological variables deviated significantly from isometry, and were negatively allometric (Table 2).

Oligoryzomys longicaudatus: The regression was significant ($R^2 = 0.85$; $F_{1,6} = 3.83$; $P < 0.001$). Three variables recovered by the model (Mallows's $P = 5.36$) were related to muscle length: Tlon, ECRad, and FDProf and 3 were related to tendon length and width: TLFCUln, and tendon length of the flexor digitorum sublimis (TLFDsubl) and TWFCRad. The RMA regression showed that 4 of the morphological variables deviated significantly from isometry, and were negatively allometric (Table 2).

Oxymycterus rufus: The multiple regression for this species was significant ($R^2 = 0.98$; $F_{1,13} = 34.569$; $P < 0.001$). Six variables entered the model (Mallows's $P = 6.9$): 3 were related to muscle length: Tlon, ECRad, and FDProf, and 3 were related to tendon length and width: tendon length of the m. extensor carpi ulnaris (TLECUln), TWECRad, and m. flexor digitorum sublimis tendon length (TLFDSubl). The RMA regression showed that 4 of the variables deviated significantly from isometry and were negatively allometric (Table 2).

Species–locomotor modes and age classes.—Multivariate analysis of covariance revealed significant differences among groups, including age classes (Wilks' $\lambda = 0.103$; $d.f. = 26, 52$; $P < 0.001$), species (i.e., locomotor mode; Wilks' $\lambda = 0.005$; $d.f. = 75, P < 0.001$), and the age class by species interactions (Wilks' $\lambda = 0.004$, $d.f. = 150, P < 0.002$). The FDR test showed that both age classes and species were significantly different for 7 of the morphological variables (q -values < 0.05). These 7 variables were: Tlon, BB, B, TWEDCom, TLFDProf, FCRad, and FDSubl (Fig. 3).

M. triceps longus: The postnatal growth pattern of the m. triceps longus was similar in the quadrupedal saltatorial *Eligmodontia* and the semifossorial *Oxymycterus*. Muscle growth was negatively allometric early in ontogeny, reached a peak in young adults and then grew isometrically until adulthood. This trend was most pronounced between juveniles and young adults. In *Oligoryzomys*, this muscle showed a decrease in growth rate during the transition between juveniles and young adults, followed by stasis until adulthood. In *Akodon*, there was an increase in the growth rate early in ontogeny and a peak in young adults (Fig. 3A).

M. biceps brachii: The growth pattern for the m. biceps brachii was similar in *Eligmodontia* and *Oxymycterus*. Muscle growth was negatively allometric throughout postnatal ontogeny. In *Oligoryzomys*, this muscle showed a decrease in growth rate in the transition from juveniles to young adults, followed by stasis through to adulthood. In *Akodon*, m. biceps showed a pattern of isometric growth until early adulthood, followed by decreased growth until adulthood (Fig. 3B).

M. brachialis: The growth patterns of m. brachialis were similar in *Eligmodontia*, *Oligoryzomys*, and *Oxymycterus*. Muscle growth was negatively allometric throughout postnatal

ontogeny. In *Akodon*, this muscle showed a pattern of slight growth until early adulthood, and then decreased growth rate in adulthood (Fig. 3C).

M. extensor digitorum communis tendon width: This tendon widened slowly during postnatal ontogeny in *Oxymycterus*. In *Eligmodontia* and *Akodon*, it showed delayed widening in the transition between juveniles and young adults, and then widened significantly until adulthood. In *Oligoryzomys*, this tendon showed a rapid increase in width until early adulthood and then an abrupt decrease in adults (Fig. 3D).

M. flexor digitorum profundus tendon length: In *Akodon*, *Eligmodontia*, and *Oxymycterus*, the length of this tendon showed a decreased growth rate during the transition from juveniles to young adults followed by stasis until adulthood. Conversely, in *Oligoryzomys*, this tendon elongated rapidly throughout postnatal ontogeny (Fig. 3E).

M. flexor carpi radialis: This muscle grew slowly in *Akodon* during postnatal ontogeny and showed a similar pattern in the other 3 species, that is, there was slow growth until early adulthood. Subsequently, *Oxymycterus* and *Eligmodontia* exhibited isometric growth while *Oligoryzomys* showed a decreased growth rate (Fig. 3F).

M. flexor digitorum sublimis: This muscle showed delayed growth during postnatal ontogeny in *Oxymycterus*, while in the other species there was isometric growth until early adulthood followed by a slower growth rate until adulthood. This pattern was most pronounced in *Oligoryzomys* (Fig. 3G).

DISCUSSION

We investigated patterns of allometry across 3 age classes for the muscles and tendons of the forelimb in 4 sigmodontine rodent species representing 4 locomotor modes. In an evolutionary sense, morphology is a reflection of both static and ontogenetic allometric patterns (Shingleton 2010). The general allometric pattern revealed by our data is one of negative allometry (i.e., relative shortening with increasing body size), because most of the morphological variables had regression coefficients less than 1 (Table 2). Muscles tend to elongate with negative allometry independently of species.

Studies of felids (Cuff et al. 2016a, 2016b) have proposed that many of the muscles involved in limb and body support should scale with positive allometry, making muscles more adept at supporting increasing body masses. Cuff et al. (2016a) found that larger felid species have relatively weaker anterior postcranial musculature compared with smaller species, due to an absence of significant positive allometry. The general pattern of negative allometry for our morphological variables suggests a similar pattern exists in the forelimb musculature of sigmodontine rodents. It is possible that growth in musculo-tendinous system is constrained by allometric growth of bones during ontogeny; this constraint may be less problematic in rodents than in felids because of their smaller size. In fact, Comer (1956) indicated that during the postnatal ontogeny of rats, the length of the gastrocnemius muscle was determined by

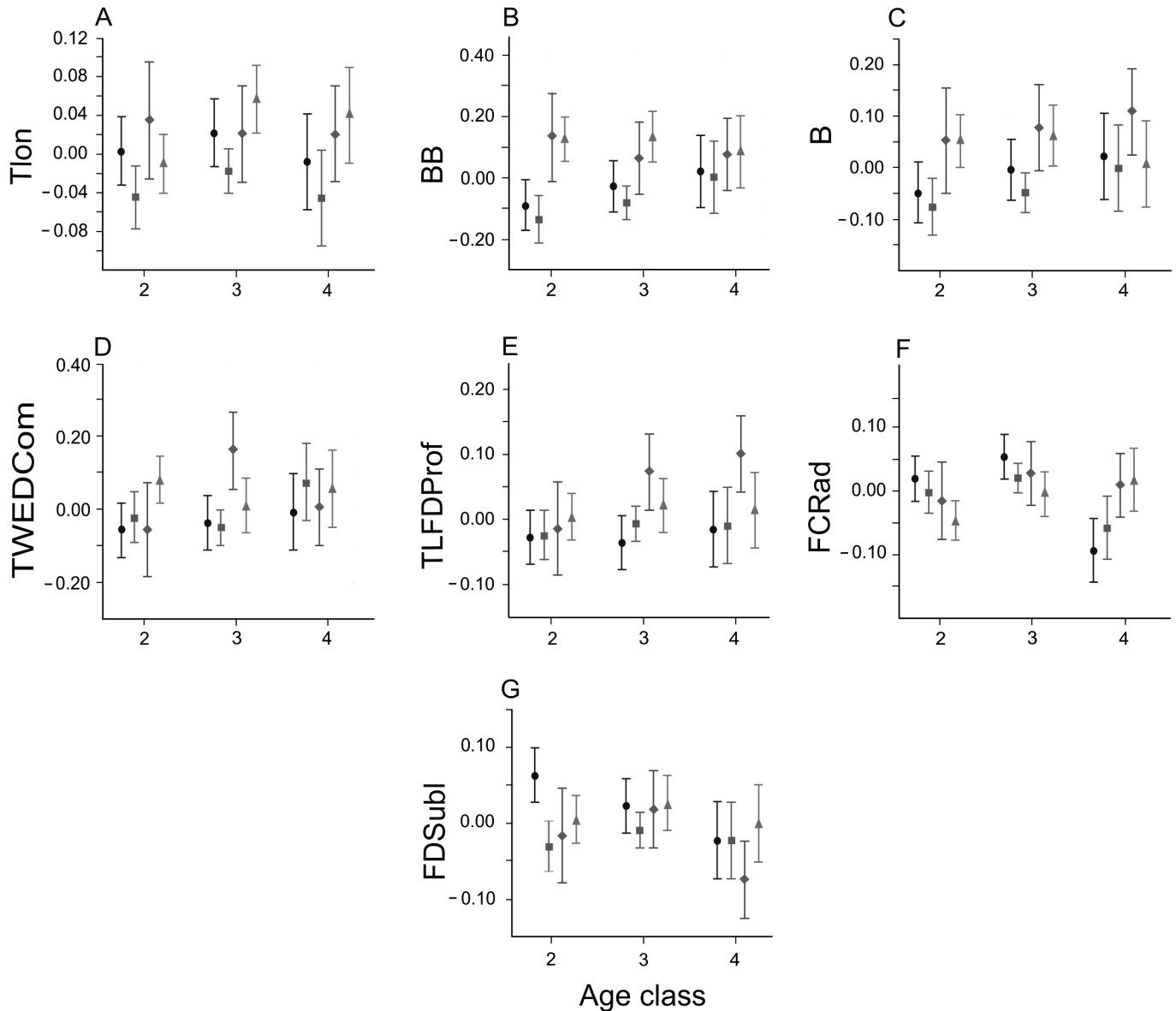


Fig. 3.—Box-and-whisker plots of 7 morphological variables by age class (2 = juvenile; 3 = young adult; and 4 = adult). Symbols indicate mean values; whiskers represent variances for each muscle or tendon. Note that the extensor and flexor muscles have similar ontogenetic trajectories in the quadrupedal saltatorial *Eligmodontia* and in the semifossorial *Oxymycterus* (A, B, C, F, and G). Scansorial *Oligoryzomys* has a significantly greater growth rate of length and width of the tendons than those of the other species—locomotor modes (D and E). The species studied are indicated by symbols: triangle, *Akodon caenosus*, ambulatory; square, *Eligmodontia typus*, quadrupedal saltatorial; diamond, *Oligoryzomys longicaudatus*, scansorial; and circle, *Oxymycterus rufus*, semifossorial. Abbreviations for morphological variables: Tlon, m. triceps longus; BB, m. biceps brachii; B, m. brachialis; TWEDCom, m. extensor digitorum communis tendon width; TLFDFProf, length of the tendon of m. flexor digitorum profundus; FCRad, m. flexor carpi radialis; FDSubl, m. flexor digitorum sublimis.

the range of motion and length of the tibia, while tendon length was demonstrated to be independent of those factors.

The negative allometric patterns we observed for morphological variables in all taxa are inconsistent with the general ideas of De Koning (1987) that the amount of muscular tissue increases more than tendinous tissue, at least in sigmodontine rodents. The hypothesis of De Koning (1987) has been supported by data from hindlimbs of rabbits and felids (see also Ingelmark 1945; Elliott 1965; Tamaki and Uchiyama 1995; Cuff et al. 2016b), indicating perhaps that differential growth of muscles and tendons is related to

phylogenetic constraints rather than functional or ecological requirements.

Eilam (1997) suggested that heterochrony explains the diversity of body forms in several rodent taxa, and it has been noted as an important process affecting morphological diversity in mammals (Ravosa et al. 1993; Maunz and German 1997; Richardson et al. 2009), and seems to modulate musculo-tendinous growth. Positive allometric muscle growth combined with negative allometric growth of tendon length would result in a limb segment consisting primarily of muscle fibers. Alternatively, isometric growth of tendon

length combined with negative allometric muscle growth would produce a limb segment consisting primarily of long tendons. This provides a simple model for the divergent patterns seen in the forearms of bats or horses and that of a rat. However, the fact that our data demonstrate primarily negative allometric growth suggests that other skeletal elements should be considered. It may be that relative shortening of the musculo-tendinous components is an adjustment to the rate of bone growth (see also Comer 1956; Cuff 2016a, 2016b). In fact, our results are consistent with the observations of Huang et al. (2015) for mouse mutants (Spotch delayed [Spd] mice—Vogan et al. 1993). They found that in the E12.5 stage, muscles spanned the entire length of the short zeugopod and long tendons within the zeugopod only became apparent at stage E13.5, with tendon elongation occurring in later stages along with zeugopod skeletal growth. It is reasonable to infer the same dependence on skeletal growth occurs in later ontogenetic stages. The dependence between musculo-tendinous structures and bones in embryonic phases contrasts with data from studies of skull growth and body architecture in rodents, including sigmodontine rodents, that demonstrate independence between embryonic and postnatal phases (Zelditch 1988; Hingst-Zaher et al. 2000; Zelditch et al. 2003; Willmore et al. 2006). These contrasting results may be evidence that the cranium and postcranium belong to different developmental and evolutionary modules.

Our results showed significant differences for 7 morphological variables (5 muscles and 2 tendons). Three of the muscles are flexors and extensors of the forearm (i.e., triceps, biceps brachii, and brachialis) and 1 is a flexor of the wrist (i.e., flexor carpi radialis). These show the same ontogenetic patterns in the quadrupedal saltatorial *Eligmodontia* and the semifossorial *Oxymycterus*: a proportional increase in size in the juveniles and young adult stages followed by a decrease in growth rate of the m. triceps and m. flexor carpi radialis. Lehmann (1963) and Alvarez et al. (2012) noted that the triceps brachii is enlarged in subterranean rodents *Geomys* and *Ctenomys*. We infer that this enlargement may be a consequence of isometric growth until early adulthood, followed by negative allometry. Interestingly, the biceps brachii and brachialis muscles show positive allometry throughout postnatal ontogeny. The growth pattern of these muscles is shared by the quadrupedal saltatorial *Eligmodontia* and the semifossorial *Oxymycterus* until stage 3. After this stage, muscle growth rates diverge, perhaps because the developmental constraints have eased. These muscles play an important role in stabilizing the elbow and in the complex movements of the forelimbs in fossorial and quadrupedal saltatorial animals (Vassallo 1998; Morgan and Verzi 2006; Samuels and Van Valkenburgh 2008; Carvalho Coutinho et al. 2013; Fuentes et al. 2013). Thus, the ontogenetic trajectories of the primary flexor and extensor muscles of the forearm suggest that these muscles are functional early in postnatal ontogeny.

In *Oligoryzomys*, the m. triceps and m. biceps brachii show a similar trend: weak positive allometry until the third ontogenetic stage, with subsequent isometry. Alternatively, the m. brachialis grows isometrically throughout its ontogeny. Perhaps

the greater volume of the m. triceps relative to the m. biceps brachii and m. brachialis (Holzbaur et al. 2007) necessitates isometric growth in order to assure balance between antagonistic muscles. A similar explanation may be provided for isometric growth of the flexor digitorum sublimis muscle in the semifossorial *Oxymycterus*. This large muscle may require balanced growth with other smaller muscles.

Ono et al. (1993) showed that elongation of muscle fibers in chickens is a factor that controls muscle growth. Cessation of muscle growth is synchronous with cessation of bone growth. They observed a different rate of enlargement for different fiber types. This may explain the variety of muscle growth patterns observed in our study, such as the continuous isometric growth of the m. brachialis relative to the m. flexor digitorum sublimis. Patterns of allometry in the musculo-tendinous system may represent adaptations to specific habitat requirements as demonstrated by Bryden (1973) on the muscular growth pattern of the southern elephant seal (*Mirounga leonina*). These animals experience large changes in habitat use and locomotor mode as they transition from terrestrial to aquatic habitats with increased relative growth of specific structures for each habitat. Similarly, Carrier (1983) showed that black-tailed jackrabbits (*Lepus californicus*) undergo early ontogenetic changes including positive muscle allometry related to enhanced cursorial locomotion.

Lessa and Stein (1992) and Carrizo et al. (2014) showed that fossorial rodents exhibit broader insertion tendons of the m. extensor digitorum communis in order to achieve greater forces for forelimb extension during digging. Our data suggest that this width is reached by isometric growth throughout the ontogenetic sequence. Interestingly, the most divergent pattern is shown by *Oligoryzomys*, with positive allometry between stages 2 and 3, followed by an abrupt slowdown between stages 3 and 4. One of the primary roles for this muscle in scansorial species is retraction of the claws during climbing. The pattern we observed suggests that the extensor tendons elongate early in ontogeny, possibly to assure efficiency in climbing. Carrizo et al. (2014) showed that scansorial sigmodontines tend to have longer tendons for the m. flexor digitorum profundus. Our data show that these tendons exhibit a rather steady and constant growth throughout their ontogeny. This may indicate that scansoriality is a locomotor type that requires long tendons in all developmental stages assuring appropriate wrist and digit flexion during climbing (Cartmill 1985).

We provide data on allometric patterns of the musculo-tendinous complex of the forelimb in sigmodontine rodents, and assess patterns of static allometry. We compared these patterns across 4 species associated with different locomotor modes. The patterns differed among species, and hence among locomotor modes. The strongest patterns were associated with muscles and tendons related to extension of the arm and flexion of the wrist. Future analyses on morphology and allometry of the limb bones are needed to understand the functional integration of the muscle–tendon–bone system during postnatal growth and locomotor development in sigmodontine rodents.

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SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Morphological variables of the muscles and tendons of the forelimb of 4 sigmodontine rodents reported as mean and standard deviation ($\bar{X} \pm SD$) and with age class indications. *N*: represents number of individuals per species. Muscle abbreviations are provided in [Table 1](#).

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APPENDIX I

List of sigmodontine specimens examined. Acronyms for Argentinian institutions where voucher specimens are deposited and personal catalogs are as follows: **MACN**, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires, Argentina; **MLP**, Museo de La Plata, La Plata. **JPJ**: field number of J. Pablo Jayat to be deposited at MACN; **UP**: field number of Ulyses Pardiñas and **PPA**: Project Patagonia Agencia; **W/D**, without data.

Akodon caenosus ($n = 17$): **JPJ** (28, 45, 10, 35, 200, 156, 159, 93, 29, 191, 212, 10, 166, 15, 506); **MACN** (25866, 25867).

Eligmodontia typus ($n = 24$): **PPA** (1062, 1044, 1064, 1050, 573, 587, 582, 115, 117, 111, 468, 469, 417); **MACN** (13536, 13539, 14561, 14564, 14562, 19312, 19318, 25886); **MLP** (3.X.70.81). Two specimens **W/D**.

Oligoryzomys longicaudatus ($n = 8$): **MACN** (23331, 19268, 19264, 19262). Four specimens **W/D**.

Oxymycterus rufus ($n = 15$): **UP** (339, 343, 332, 331, 323, 305, 329); **MACN** (14959, 15015, 26620, 26621); **MLP** (3.X.00.09, 3.X.00.10, 2.X.70.62, 19.VI.02.17).